Successional patterns in mosses, lichens and other plants on fallen trees in a tropical cloud forest

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Abstract: A diverse assemblage of species proliferate on the decaying substrate of a fallen tree. As decay progresses and the microhabitat of the fallen tree changes, the relative abundance of different growth forms may change in a predictable way with changes in the availability of light, water, and nutrients. This study tested whether the level of decay was related to the diversity and abundance of plant growth forms on fallen trees in the premontane wet forest of Monteverde, Costa Rica. On 25 fallen trees, five in each of five levels of decay, we recorded the proportion of 2 m transects covered by one of nine growth forms. The number of growth forms increased with level of decay, but with different patterns. The abundance of mosses and lichens were strongly related to the level of decay. Mosses were dominant in the first level of decay, decreased in the second and increased in subsequent levels of decay. Lichen abundance displayed a pattern that was nearly opposite to that of moss. The increase in number of growth forms over time suggests that microhabitat conditions and resource availability on decaying trees changes over time, and that the abundance of different growth forms fluctuate in response. The plant community that grows upon fallen trees seems to follow a predictable succession over time.

Key Words: decay, nutrient availability

Introduction

Fallen trees provide substrate, habitat, and resources for many organisms in tropical forests. The physical and biological characteristics of fallen trees seem to follow a predictable succession. The environment provided by fallen trees changes over time with respect to moisture, temperature, light availability, and the biotic community, especially soil microbes, microflora, and fauna (Barbour et al. 1987). With increasing time, the gap created in a tree fall closes, thus decreasing light availability. In addition, increasing level of decay also increases water content and the potential for additional new colonizers upon the fallen tree. A diverse assemblage of species proliferate on the decaying substrate of a fallen tree, including mosses, lichens, liverworts, and herbaceous and woody plants.

Initially, plant species composition is influenced by colonization events. However, as decay proceeds and available substrate space decreases, competition between plants should intensify and competitive exclusion should increasingly determine community composition on the fallen tree. Thus, the relative abundance of different plant growth forms on fallen trees may change in a predictable way in response to sequential changes in abiotic factors (availability of light, water, and nutrients) and the biotic environment (the pool of plant species with propagules reaching the fallen tree substrate).

This study explored patterns in the plant communities that colonize fallen trees, and tested whether the level of decay (a proxy for time since the tree fall) was related to the diversity and abundance of plant growth forms in the premontane wet forest of Monteverde, Costa Rica. We predicted that the number of plant growth forms would generally increase with the level of decay of a fallen tree, but that two common growth forms in cloud forests, mosses and lichens, would respond differently due to differences in their relative dependence on light and water. Mosses generally require high moisture environments while lichens tend to require relatively high sunlight (Hansel et al. 1996).

Methods

We sampled fallen trees within 10 m of the trails in the tropical lower montane rainforest near the biological station at Monteverde, Costa Rica (1550 - 1650 m asl). We haphazardly selected five fallen trees within each of five levels of decay. These were, in ascending order of decay, 1) recently fallen with branches and twigs, 2) recently fallen with branches but no twigs, 3) bark but no branches or twigs, 4) bole starting to lose bark and slightly punky (i.e., soft) to the touch, 5) bole punky to the core of the trunk. All trees had a trunk diameter > 30 cm (mean ± SD = 58.3 ± 29.7 cm).

For each fallen tree, we randomly selected a point at which to begin two 2 m transects along the top and side of the trunk (alternating between left and right sides of the trunk). We recorded the distance along the transect occupied by each of the following growth forms: mosses, lichens, herbaceous plants, liverworts, vines, fungi, epiphytes, and trees. In addition, we recorded the distance of unoccupied area along each transect.

The number of growth forms at each level of decay was calculated by pooling the total number of growth forms occurring at each level on one or more of 5 fallen trees. We examined the relationship between number of growth forms and level of decay within each location by linear regression. We compared temporal patterns in mosses and lichens with an analysis of variance that included tree decay (5 classes), transect location (side vs. top), and plant form (mosses or lichens) as independent variables and proportion of surface area occupied by either plant form as the dependent variable. Proportion data were arcsine transformed for these analyses.

Results

There was a significant positive relationship between number of plant forms and the level of decay, but no difference between transects on the top and side of fall trees (Fig. 1). Moss coverage decreased as fallen trees reached the second level of decay and aver-

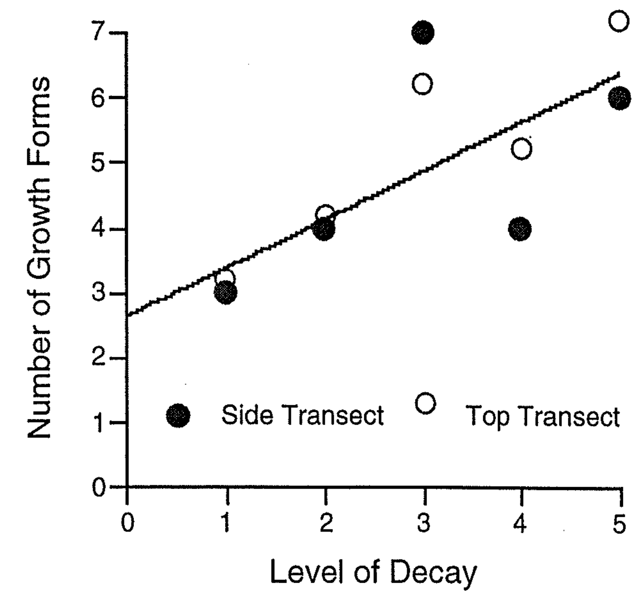

Figure 1. Relationship between number of growth forms and decay stage on the top and side of fallen trees at Monte Verde Biological Station, Costa Rica (r^2 = 0.54, $F_{1,8}$ = 9.33, p = 0.016). Regressions fit seperately to top and side did not differ from one another. Sampling recognized eight possible growth forms.

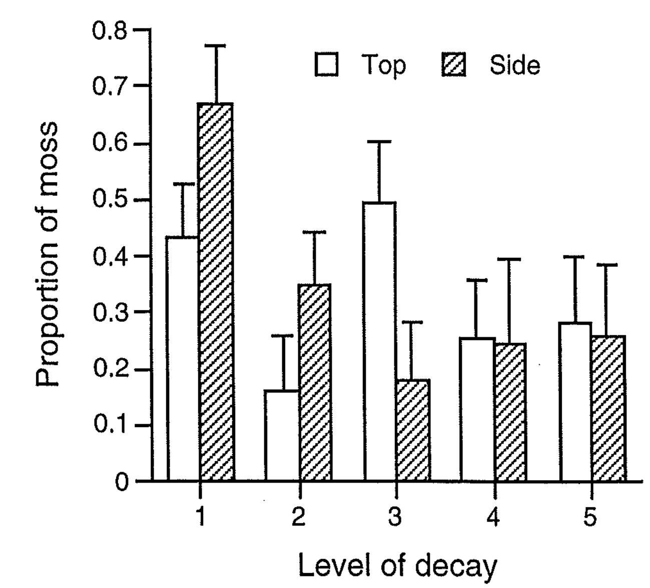

Figure 2. Mean proportion (± SE) of moss coverage on the top and side of fallen trees with increasing levels of decay in montane forest of Monte Verde, Costa Rica.

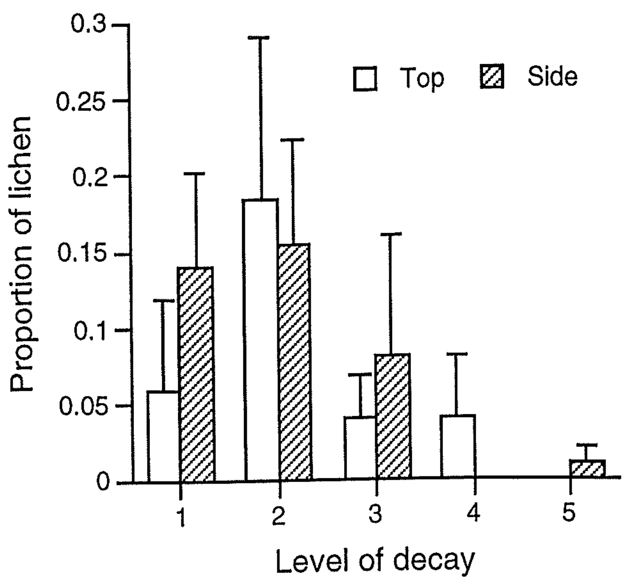

Figure 3. Mean proportion (± SE) of lichen coverage on the top and side of fallen trees with increasing levels of decay in montane forest of Monte Verde, Costa Rica.

aged ≈30% through the subsequent levels of decay (Fig. 2). In contrast, lichen coverage increased from the first to the second decay level, and then declined to less than 2% by the fifth level (Fig. 3). Analysis of variance indicated strong main effects of level of decay and growth form (mosses or lichens), and a nearly significant interaction between level of decay and growth form, in predicting the proportion of surface area occupied by either mosses or lichens (Table 1).

Discussion

Increases in the number of plant growth forms with increasing decay level of fallen trees suggests that microhabitat conditions on the decaying tree are changing over time. This increase in growth forms may be due to changes in resource availability (especially water and minerals) as a result of increased porosity of the wood (Barbour et al. 1987), and may also be influenced by the increasing likelihood over time that plant propagules will have reached the log.

The abundance of moss and lichens changed with decay level, but in different ways. Mosses decreased initially, then increased in later levels of log decay. This pattern may be related to changes in light availability when gaps are formed; light intensity tends to be high during the first and second decay levels of fallen trees, but then decreases as the canopy closes during subsequent levels of decay. Therefore, moss abundance may initially decline due to dessication from the light intensity. Hansel et al. (1996) observed a decrease in moss coverage and an increase in lichen coverage with increasing canopy openness, which seems comparable to changes in the moss and lichen abundance between the first two levels of decay in our study. As decay continues, the fallen tree begins to retain more water and receive less light, which may make the fallen trees increasingly unsuitable for lichens. The decrease in lichens may allow moss species to colonize the fallen tree, and perhaps these are different species than those that were initially present. Hansel et al. (1996) documented an increase in moss coverage and decrease in lichen coverage with increasing moisture levels, which parallels the changes in moss and lichen abundance that we measured in the later levels of decay when the fallen trees were becoming increasingly water-saturated.

The succession of growth forms on fallen trees at Monteverde illustrates the complexity of the microhabitat created on decomposing trees, but also indicates that there are predictable, repeatable patterns in the succession of plant communities that occupy fallen trees. The increase with decay level of growth form diversity probably influences the fallen tree microhabitat by further increasing water and nutrient content, which could accelerate decomposition of the fallen tree. This, in turn, would create positive feedback by promoting more plant growth. Future studies might explore changes in microorganism composition with increasing level of decay, and how these patterns relate to successional transitions between plant growth forms on decomposing trees.

Table 1. Analysis of variance results testing the effects of level of decay, transect location (top or side of fallen tree), growth form present (mosses or lichens) on the mean proportion of surface area occupied.

Source	df	Mean Squares	F	P
Decay	4	0.336	3.91	0.006
Location	1	0.001	0.02	0.899
Growth Form	1	3.989	46.46	<0.001
D x L	4	0.143	1.66	0.168
D x G	4	0.200	2.32	0.064
L x G	1	0.007	0.08	0.774
D x L x G	4	0.089	1.03	0.397
Error	80	0.086		

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